

Importance of forest structures on four beetle families (Col.: Buprestidae, Cerambycidae, Lucanidae and phytophagous Scarabaeidae) in the Areuse Gorges (Neuchâtel, Switzerland)¹

Sylvie BARBALAT

Institut de Zoologie, Emile Argand 11, CH-2007 Neuchâtel, Switzerland.

Importance of forest structures on four beetle families (Col.: Buprestidae, Cerambycidae, Lucanidae and phytophagous Scarabaeidae) in the Areuse Gorges (Neuchâtel, Switzerland).

- The species richness and abundance of selected xylophagous (Buprestidae, Cerambycidae and Lucanidae) and rhizophagous or saprophagous beetles (phytophagous Scarabaeidae) were compared between various forest stands with different ecotone structures. Window traps and water traps were used to sample the beetles. Among the 65 captured species, 13 belonged to the Buprestidae, 41 to the Cerambycidae, 8 to the phytophagous Scarabaeidae and 3 to the Lucanidae. Forest stand and ecotone type were found to have a significant influence on these beetle communities. In oak stands, typical species such as *Plagionotus arcuatus*, *Anoplodera sexguttata* or *Anthaxia salicis* were found, while in beech forests *Platycerus caprea* was found as a characteristic species. Natural edges are characterised by grassland and shrub species such as *Agapanthia violacea*, *Phytoecia cylindrica* and *Anthaxia nitidula*. In artificial clearings, species living in old stumps such as *Corymbia rubra*, *Prionus coriarius*, *Rhagium bifasciatum*, or *Anastrangalia sanguinolenta* are common as well as species living in the small branches left after a cutting, the most common of which being *Stenurella melanura*. In order to conserve a high diversity of forest beetles, oaks should be favoured (it hosts 9 typical species in our study) and diversified structures such as natural edges and artificial clearings must be maintained or created.

Key-words: Forest ecology - Buprestidae - Cerambycidae - Scarabaeidae
Pleurosticti - Lucanidae - Swiss Jura - Bioindicators.

INTRODUCTION

Buprestids, cerambycids and lucanids have xylophagous larvae (DAJOZ 1980). Depending on the species, the larvae can colonise living trees, dead wood or rotten stumps. On the other hand, phytophagous scarabaeids are rather rhizophagous or saprophagous as larvae and phytophagous as adults (ALLENSPACH 1970).

¹ This paper is part of the author's PhD.

Manuscript accepted 23.03.1998

Xylophagous beetles are an important element of forest ecosystems. They actively participate in dead wood decomposition. The larval galleries facilitate wood colonisation by micro-organisms, which considerably increases their efficiency (DAJOZ 1980).

Thanks to museum collections, it has been possible to elaborate the rarefaction of several, mainly spectacular, species since the end of the last century, although the forest surface in Switzerland has not decreased during that time. The decline of many species can be attributed to coniferous tree plantings at low altitude, mainly spruce (*Picea abies*), instead of broad-leaved tree forests, causing a considerable loss of habitats for lowland species (SPEIGHT 1989). Forest trees are cut down before reaching an age at which they become attractive for xylophagous fauna and isolated old trees have almost disappeared. Regression of traditional orchards and humid habitats has also caused the rarefaction of specialized species (GEISER 1984). For species colonizing more open biotopes, mainly among scarabaeids, agriculture intensification has also been a cause of decline (ALLENSPACH 1970).

Some authors have worked on the influence of forest structures as well as woodland type on beetle communities. In Poland, for instance, GUTOWSKI (1986) compared the fauna of a virgin forest with the fauna of a managed one. The changes in communities of cambio- and xylophagous insects in different age classes of forest stands have also been studied (STARZYK 1977; STARZYK & WITKOWSKI 1981; GUTOWSKI 1995). STARZYK (1976; 1979) and GUTOWSKI (1985) have studied the cerambycid communities occurring in different forest associations.

In Switzerland, the importance of dead wood quantity for xylophagous beetles was underscored by HARTMANN & SPRECHER (1990). BARBALAT (1996) and BARBALAT & BORCARD (1997) have shown the importance of artificial clearings on xylophagous beetles in managed forests.

The aim of this work is to study, among different edges and clearings, what structures are most favourable for this fauna, in order to be able to make proposals to promote a forest management respecting biodiversity as much as possible. If buprestids, cerambycids and lucanids are good indicators for forest biotopes, only a few species are adapted to forest edges. For this reason, we consider as well a family, the scarabaeids, linked to more open habitats.

MATERIALS AND METHODS

STUDY AREA

Our study was carried out in the Areuse Gorges near Neuchâtel (Western Switzerland) on the first Jura slopes (Fig. 1). We chose twelve sites in three forest types: oak, beech and mixed stands. Mixed forests are usually constituted of broad-leaved trees such as beech, oak and maple (*Acer pseudoplatanus*) mixed with coniferous trees such as spruce, pine and fir (*Abies alba*). These mixed forests are usually located on thin calcareous soils where tree growth is weak. In these stands, foresters create artificial clearings ranging from 650 to 10.000 m², in order to favour pines which grow quite well on shallow soils and require much light to grow. In these

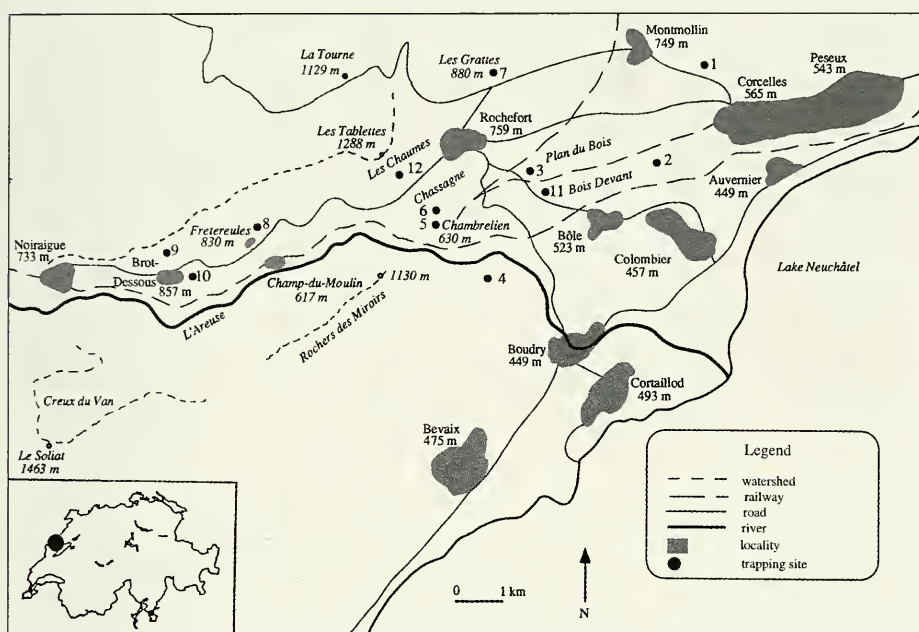


FIG. 1. Study area. After BARBALAT (1997)

station	locality	coordonnates	altitude	expo	slope	forest type	cover	habitat type	edge type
1	Corcelles	556125 204250	695 m	S	20%	oak	80%	edge	natural
2	Colombier, Chanet	555600 202950	555 m		0%	beech	40%	artificial clearing	clean
3	Chambrelieu, Plan du Bois	553250 202700	670 m	SE	40%	mixed	60%	artificial clearing	clean
4	Boudry, Chanet	553000 201150	550 m		0%	oak	30%	artificial clearing	clean
5	Chambrelieu, Chassagne	552000 201900	725 m	SE	20%	mixed	40%	artificial clearing	clean
6	Chambrelieu, Chassagne	551900 202250	770 m	SE	15%	mixed	60%	artificial clearing	clean
7	Rochefort, Les Grattes	552470 204070	880 m	SE	80%	mixed	40%	edge	natural
8	Frèrezeules	549050 201600	860 m	SE	45%	beech	90%	edge	natural
9	Brot-Dessous	547600 200950	890 m	S	40%	beech	90%	edge	clean
10	Brot-Dessous	547850 200900	790 m	S	40%	beech	50%	natural clearing	natural
11	Chambrelieu, Bois-Devant	553500 202450	620 m	SE	15%	mixed	70%	artificial clearing	clean
12	Rochefort, Chaumes	551375 202625	840 m	SE	60%	beech	70%	artificial clearing	clean

expo = exposure; cover = tree cover.

TABLE 1. Site description. After BARBALAT (1997)

clearings all the trees are cut down except a few selected pines, which are left for their seeds. Similar clearings are also created in oak stands in order to favour these trees which also need much light for their growth. This type of clearing is not made in beech forests, because beech can grow in more shady conditions. All the sites have been chosen either in clearings or forest edges with South or South-East exposure (Table 1).

Species	Author	Distribution	Level	Habitat	Main host plants	Site
BUPRESTIDAE						
<i>Agrius angustulus</i>	(Ill., 1803)	euro Siberian, NA	col	broad/tran	<i>Quercus</i>	1,2,3,4,6,8,10,11
<i>Agrius biguttatus</i>	(F., 1777)	holomediterranean	col	broad/tran	<i>Quercus</i>	1,2,3,4,5,10,11,12
<i>Agrius cyanescens</i>	Ratzb., 1837	european	col-mon	broad/tran	<i>Lonicera</i>	10
<i>Agrius laicornis</i>	(Ill., 1803)	european, ME	col	broad/tran	<i>Quercus</i>	3,4,7
<i>Agrius olivicolor</i>	Kiesw., 1857	euro Siberian	col	broad/tran	<i>Corylus</i> , <i>Carpinus</i>	2,5
<i>Agrius sulcicollis</i>	Lacord., 1835	euro Siberian	col	broad/tran	<i>Quercus</i>	1,2,3,4,6,7,11
<i>Agrius viridis</i>	(L., 1758)	euro Siberian	col-mon	broad/tran	broadl	2,3,4,5,8,11,12
<i>Anthaxia helvetica</i>	Stierl., 1868	mountain	col-sub	conif/tran	conif	1,2,3,4,5,6,7,8,9,10,11,12
<i>Anthaxia nitidula</i>	(L., 1758)	holomediterranean	col-mon	tran/orch	<i>Prunus</i>	1,7
<i>Anthaxia quadripunctata</i>	(L., 1758)	mountain	mon-sub	conif/tran	conif	1,2,3,5,6,7,11,12
<i>Anthaxia salicis</i>	(F., 1777)	holomediterranean	col	broad/tran	<i>Quercus</i>	1,4
<i>Anthaxia similis</i>	Saund., 1871	mountain	mon-sub	conif/tran	conif	3,6,11
<i>Chrysobothris affinis</i>	(F., 1794)	euro Siberian, NA	col-mon	broad/tran	broadl	1,2,3,4,8,9,11
SCARABAEIDAE						
<i>Amphimallon atrum</i>	(Hbst., 1790)	W. european	col-mon	open/tran	?	7,8,9,10
<i>Cetonia aurata</i>	(L., 1761)	paleartic	col-sub	broad/tran	broadl	3,4,7,8,11
<i>Hoplia argentea</i>	(Poda., 1761)	C. and S. european	col-sub	open/tran	?	4,5,8,9,10
<i>Onaloplia ruficollis</i>	(F., 1775)	C. european	col-mon	open	Poaceae, div	10
<i>Phyllotreta horticola</i>	(L., 1758)	euro Siberian	col-sub	open/tran	div	1,3,4,6,7,8,9,10,12
<i>Rhizotrogus aestivus</i>	(Ol., 1789)	pontomediterranean	col-mon	open/tran	div	1
<i>Serica brunnea</i>	(L., 1758)	euro Siberian	col-mon	broad/tran	div	1,2,4,5,7,8,9,10,11,12
<i>Trichius fasciatus</i>	(L., 1758)	euro Siberian	col-mon	broad/tran	broadl	1,2,3,4,5,6,7,8,10,11,12
LUCANIDAE						
<i>Platycerus caprea</i>	(Deg., 1774)	C. european	mon-sub	broadl	broadl	4,7,8,9,10,12
<i>Platycerus caraboides</i>	(L., 1758)	C. european	col-mon	broadl	broadl	1,2,4,5,12
<i>Sinodendron cylindricum</i>	(L., 1758)	euro Siberian	col-mon	broadl	broadl	7
CERAMBYCIDAE						
<i>Asapanthia villosa viridescens</i>	(Deg., 1775)	euro Siberian	col-mon	open/tran	Asteraceae, Apiaceae	11
<i>Asapanthia violacea</i>	(F., 1775)	pontomediterranean	col-mon	open	Dipsacaceae	1
<i>Allosterna tabacicolor</i>	(Geer., 1775)	paleartic	col-mon	broadl	broadl	1,2,3,4,5,6,7,8,9,10,12
<i>Anaglyptus mysticus</i>	(L., 1758)	european	col-mon	broad/tran	broadl	3,5,6,12
<i>Anastrangalia dubia</i>	(Scop., 1763)	mountain	mon-sub	conif/tran	conif	2,3,4,5,6,7,10,11,12
<i>Anastrangalia sanguinolenta</i>	(L., 1761)	C. and E. european	mon-sub	conif/tran	conif	1,3,3,6,7,10,11,12
<i>Anoplodera sexguttata</i>	(F., 1775)	european	col	broad/tran	<i>Quercus</i>	1,4,5
<i>Arhopalus rusticus</i>	(L., 1758)	holarctic	col-mon	conif	conif	11
<i>Cerambyx scopoli</i>	Füssl., 1775	european, NA	col-mon	broadl/orch	broadl	10
<i>Clytus arietis</i>	(L., 1758)	european, ME	col-mon	broad/tran	broadl	1,2,3,4,5,6,7,8,9,10,11,12
<i>Clytus lana</i>	Muls., 1847	mountain	mon-sub	conif/tran	conif	2,6,7,11
<i>Cortodera femorata</i>	(F., 1787)	C. and E. european	col-sub	conif	<i>Picea</i>	1,3,12
<i>Corymbia rubra</i>	(L., 1758)	paleartic	col-sub	conif/tran	conif/broadl	1,2,3,4,5,6,7,10,11,12
<i>Dinoptera collaris</i>	(L., 1758)	paleartic	col-mon	broad/tran	broadl	6,7,8,10,12
<i>Gaurotes virginea</i>	(L., 1758)	boreo-alpine	mon-sub	conif/tran	conif	3,5,6,12
<i>Grammoptera abdominalis</i>	(Steph., 1831)	C. and S. european, ME	col	broad/tran	<i>Quercus</i> , <i>Castanea</i>	7
<i>Grammoptera ruficornis</i>	(F., 1781)	european, ME	col	broad/tran	broadl	1,2,12
<i>Leiosus nebulosus</i>	(L., 1758)	european	col-mon	broadl/mix	broadl	2,3,7,8,11,12
<i>Leptura maculata</i>	(Poda., 1761)	european, ME	col-mon	broadl/tran	broadl	1,2,3,4,5,6,7,8,9,10,11,12
<i>Molophilus minor</i>	(L., 1758)	paleartic	mon-sub	conif/mix	conif	7,9
<i>Obrium brunneum</i>	(F., 1792)	european, ME	mon-sub	conif/mix	conif	3,5,6,7,9,11,12
<i>Oxyrinus cursor</i>	(L., 1758)	E. european, ME	mon-sub	conif/mix	conif/broadl	3,6
<i>Pachytodes cerambyciformis</i>	(Schrk., 1781)	C. european, ME	col-mon	broad/tran	broadl/conif	1,2,3,4,5,6,7,8,10,11
<i>Parnena balticus</i>	(L., 1767)	W. mediterranean	col	broadl/tran	broadl	3,5,7
<i>Phymatodes testaceus</i>	(L., 1758)	holarctic	col-mon	broadl	broadl	3,4,7,9
<i>Phytoecia cylindrica</i>	(L., 1758)	paleartic	col-mon	open	Apiaceae	7,10
<i>Pidonia lurida</i>	(F., 1792)	mountain	mon-sub	conif/mix	<i>Picea</i> , <i>Fagus</i>	10
<i>Plagionotus arcuatus</i>	(L., 1758)	european, ME, NA	col	broadl/mix	<i>Quercus</i>	1,4,11
<i>Pogonocherus fasciculatus</i>	(Deg., 1775)	paleartic	col-sub	conif/tran	conif	3
<i>Pogonocherus hispidulus</i>	(Pill. Mitt., 1783)	european	col-mon	broadl/mix	broadl	5,6,12
<i>Prionus coriarius</i>	(L., 1758)	paleartic	col	broadl/mix	broadl/conif	3,4
<i>Pseudovadonia livida</i>	(F., 1776)	paleartic	col	open/tran	soil	3,5
<i>Pyrrhidium sanguineum</i>	(L., 1758)	european, NA	col	broadl	<i>Quercus</i>	1,3,7,12
<i>Rhagium bifasciatum</i>	F., 1775	european	col-mon	conif/mix	conif/broadl	5,6,7,12
<i>Rhagium inquisitor</i>	(L., 1758)	holarctic	col-mon	conif/mix	conif/broadl	2,3,6,11
<i>Rhagium mordax</i>	(Deg., 1775)	euro Siberian	col-mon	broadl/mix	broadl/conif	4,5,8,10,12
<i>Stenocorus meridianus</i>	(L., 1758)	euro Siberian	col	broadl	broadl	5,6,8,9
<i>Stenostola dubia</i>	(Laich., 1784)	C. and N. european	col-mon	broadl/tran	broadl	8,10,12
<i>Stenurella bifasciata</i>	(Müll., 1776)	paleartic	col	mix/tran	broadl/conif	1,6,7
<i>Stenurella melanura</i>	(L., 1758)	paleartic	col-mon	broadl/mix	broadl/conif	1,2,3,4,5,6,7,8,9,10,11,12
<i>Tetropium castaneum</i>	(L., 1758)	paleartic	mon-sub	conif	conif	3,7

Distribution: ME = Middle East, NA = North Africa, C. = central, E. = east, N. = north, S. = south, W. = west;

Habitat: broadl = broad-leaved forest, conif = coniferous forest, mix = mixed forest, tran = clearings and edges, open = open habitat, orch = orchard;

Level: col = colline, mon = montane, sub = subalpine; Main host plants: conif = coniferous trees, broadl = broad-leaved trees, div = diverse plants.

TABLE 2. Species list and ecological overview. Nomenclature after LOHSE & LUCHT (1992) and BENSE (1995).

	St. 1	St. 4	St. 11	St. 3	St. 2	St. 5	St. 6	St. 12	St. 7	St. 8	St. 10	St. 9	total	
<i>A. violacea</i>	10												10	
<i>R. aestivus</i>	12												12	
<i>A. salicis</i>	7	6											13	Oak
<i>A. sexguttata</i>	2	10				1							13	
<i>P. arcuatus</i>	7	4	2										13	preferring
<i>A. sulcicollis</i>	26	49	14	22	1		5		1				118	
<i>A. biguttatus</i>	32	167	19	16	2	1		2			1		240	species
<i>A. angustulus</i>	35	21	16	8	3		2				1		87	
<i>C. affinis</i>	1	6	5	4	1					3		1	21	
<i>G. ruficornis</i>	18				2			1					21	
<i>C. aurata</i>		14	1	2					2	3			22	
<i>A. villosoviridescens</i>			1										1	
<i>A. rusticus</i>			1										1	
<i>A. olivicolor</i>					3	1							4	
<i>P. caraboides</i>	1	1			11	4		1					18	
<i>A. viridis</i>		1	34	2	5	1		1		2			46	
<i>C. femorata</i>	1			1				1					3	
<i>P. livida</i>				1		1							2	
<i>S. bifasciata</i>	15						1		21				37	
<i>P. sanguineum</i>	1			3				1	2				7	
<i>A. laticornis</i>		1		1					1				3	
<i>P. balteus</i>				1		1			1				3	
<i>O. cursor</i>				1			1						2	
<i>A. nitidula</i>	1								6				7	
<i>P. coriarius</i>		1		3									4	
<i>P. fasciculatus</i>				1									1	
<i>R. inquisitor</i>			1	1	1		1						4	Artificial
<i>A. similis</i>			2	2			1						5	
<i>A. quadripunctata</i>	3		5	9	2	1	12	30	4				66	clearings
<i>A. dubia</i>		3	12	23	5	13	10	17	4		1		88	
<i>A. sanguinolenta</i>	5		16	2		7	79	17	6		1		133	and
<i>C. rubra</i>	5	52	108	48	56	38	75	25	1		3		411	coniferous
<i>P. cerambyciformis</i>	6	3	3	7	15	5	10		1	1	1		52	tree
<i>S. melanura</i>	33	222	53	180	25	673	481	184	42	9	32	21	1955	
<i>P. hispidulus</i>					1	1	1	1					3	
<i>A. mysticus</i>				1		1	1	1					4	preferring
<i>G. virginea</i>				3		1	5	3					12	species
<i>R. bifasciatum</i>						4	4	14	3				25	
<i>C. lama</i>			1		1		2		1				5	
<i>O. brunneum</i>			1	1		1	1	1	2			3	10	
<i>L. nebulosus</i>			2	1	2			1	3			1	10	
<i>T. fasciatus</i>	15	11	15	1	5	15	3	19	4	3	5		96	
<i>L. maculata</i>	21	13	28	17	5	38	60	51	3	12	28	11	287	ubiquitous
<i>C. arietis</i>	30	33	38	61	17	25	27	59	14	64	61	10	439	species
<i>A. helvetica</i>	11	15	46	31	3	43	90	30	112	7	6	3	397	
<i>A. tabacicolor</i>	9	20		27	2	25	23	13	9	13	19	17	177	
<i>T. castaneum</i>				1					1				2	
<i>R. mordax</i>		4				3		7		1	1		16	
<i>G. abdominalis</i>									2				2	
<i>P. testaceus</i>		1		2					1			1	5	
<i>S. brunnea</i>	1	4	2		2	2		1	2	18	25	6	63	Fresh
<i>H. argentea</i>		4					6			51	1	1	63	
<i>P. horicola</i>	1	2		1			1	4	13	105	10	2	139	
<i>S. cylindricum</i>									1				1	forest
<i>S. meridianus</i>						1	2			2		4	9	
<i>P. caprea</i>			1					16	12	6	19	6	60	and
<i>D. collaris</i>							1	1	3	1	11		17	
<i>P. cylindrica</i>									3		1		4	
<i>M. minor</i>									2			1	3	altitude
<i>S. dubia</i>								1		2	4		7	
<i>A. atrum</i>									2	3	6	15	26	preferring
<i>A. cyanescens</i>											1		1	
<i>C. scopoli</i>											1		1	
<i>P. lurida</i>											1		1	species
<i>O. ruficola</i>											1		1	
total	309	669	426	485	169	907	905	503	285	307	241	103	5309	

TABLE 3. Number of collected species in each station, diagonalized according to the biotopes they have been found in.

BEETLE SAMPLING AND ANALYSES

The study was conducted from the end of April until the beginning of September of 1994 and 1995. The following trapping methods were used: window traps and water traps (yellow and white) (BARBALAT 1995). Two traps of each type were placed in each site at about 20 cm above ground level for water traps and 80 cm for window traps. They operated without interruption during the whole season.

The data analysis was made by canonical correspondence analysis (TER BRAAK 1986, 1988a). The program CANOCO (TER BRAAK 1988b) was used in order to determine the most relevant environmental variables influencing species distribution in the studied sites. With this method, it is possible to extract the variance explained by one or more environmental variables introduced a priori in the analysis. These variables can be chosen by a forward selection and their significance tested by a permutation test. The following environmental variables were introduced in the analysis and submitted to a forward selection: "stand type (oak, beech, mixed)", "proportion of broad-leaved/coniferous trees", "clearing size (small, medium, large)", "altitude", "tree covering", "deadwood quantity", "ecotone type [natural edge (with bush stratum), clean edge (without bush stratum), artificial clearing]", "slope" and "young tree size (< 1m, 1-2 m, >2m)" in the clearings.

RESULTS

A total of 65 species (Table 2) were recorded in our study area: 13 Buprestidae, 41 Cerambycidae, 8 phytophagous Scarabaeidae and 3 Lucanidae. The total number of collected specimens was 5309 (Table 3).

The forward selection showed that two environmental variables ("stand type" and "ecotone type") explain a significant part of the data variation. We tested the environmental variables on each season separately as well as on both seasons together. In the three cases, the same variables ("stand type" and "ecotone type") were found significant ($p < 0.01$ for both variables in the three cases). Axis 1 explains 16.8 % of the variance in 1994, 20.7 % in 1995 and 18.9 % when both years are cumulated. For the second axis, these values are 16.3 %, 17.7 % and 17.7 % respectively. For this part of the analysis, the rare species (less than 3 specimens) were excluded.

The effect of the year of capture on our results has also been tested. It represents only 3.4 % of the variance ($p = 0.74$; NS). The beetle communities can therefore be considered as stable during our two trapping seasons. Table 3 shows the species richness and abundance. It was diagonalized according to the different biotopes.

Fig. 2 shows the species and sites distribution on the first two canonical axes.

DISCUSSION

BIOLOGICAL INTERPRETATION

Several of the tested variables were found collinear and our significant variables have to be considered as synthetic. The variable "stand type" is in fact correlated with the altitude, which implies not only a climatic and vegetation change but also diffe-



FIG. 2. Diagram showing species and sites distribution along the first two canonical axes, representing a linear combination of the synthetic variables "oak stand" and "artificial clearing". The variables "beech stand", "altitude" and "mixed forest" were added a posteriori as passive variables for heuristic purposes.

rences in meadow management. The other significant variable "ecotone type" is also related to other variables such as the number of coniferous trees (mainly pine) in a stand, implying specialized forest management.

On the plane formed by axes 1 and 2, it was possible to identify the three following groups: sites 7, 8, 9 and 10, sites 2, 3, 5, 11 and 12 and sites 1 and 4.

On the left end of axis 1, the variance of which is mainly due to stand type, we find sites 8, 9 and 10 located at a higher altitude in pure beech forests. Site 7 is located in a mixed forest but at a similar altitude. The only species which can be considered as a beech forest indicator is the lucanid *Platycerus caprea*, which usually lives in old stumps in mountain mixed beech forests (KOCH 1992).

The other species found in these four sites seem more related to the edge itself than to the forest type. For instance, the larvae of the scarabaeids *Serica brunnea* and *Phyllopertha horticola* are rhizophagous on many plants and the adults are phyllophagous on diverse plants, including trees. *Serica brunnea*, *Hoplia argentea* and *Amphimallon atrum* are more common in hilly or mountainous regions (HORION 1958; ALLENSPACH 1970). Their abundance in these sites could also be due to a more extensive agriculture, using less pesticides than in the lowlands.

At the other end of the first axis, sites 1 and 4 are located in almost pure oak stands, which is clearly indicated by species developing mainly in oaks, such as the cerambycids *Plagionotus arcuatus* and *Anoplodera sexguttata* as well as the buprestid *Anthaxia salicis*.

Sites 2, 3, 5, 6, 11 and 12 are in the middle of the first axis and are either located in mixed forests (sites 3, 5, 6 and 11) or in beech stands with some coniferous trees (sites 2 and 12).

Axis 2, the variance of which is principally due to the clearing type, shows an opposition between sites 1, 4, 7, 8, 9 and 10 on the top of the diagram and sites 2, 3, 5, 6, 11 and 12 on the bottom. All the "top" sites except site 4 are located in edges while all the "bottom" sites are in artificial clearings. On the top of the diagram, beside *Hoplia argentea*, *Amphimallon atrum*, *Serica brunnea* and *Phyllopertha horticola*, we can quote as edge indicators the cerambycid *Agapanthia violacea* and *Phytoecia cylindrica*, the scarabaeid *Rhizotrogus aestivus* and the buprestid *Anthaxia nitidula*.

The five scarabaeids live in open or in half open habitats. They are typical for edges without indicating if they are natural or clean. *Agapanthia violacea* and *Phytoecia cylindrica* cannot really be considered as typical edge species because their host plants can be found in other biotopes such as meadows or embankments. Nevertheless, in our case, we would tend to consider these two species as natural edge indicators. Actually meadows are usually mown quite early in the season, often before the beetle emergence. The use of fertilizers leads to the disappearance of certain typical oligotrophic and mesotrophic lawn plants which, among others, host *Agapanthia violacea* and *Phytoecia cylindrica*. In our study area, we should therefore consider that these two species can only live where the edge is wide enough to allow the maintenance of their host plants.

The only species, which can be considered as a typical edge species is the buprestid *Anthaxia nitidula*, which lives in treelike Rosaceae and which is often found on *Crataegus* sp., *Prunus spinosa* or *Rosa canina*, which are typical edge shrubs.

On the bottom of the diagram, we find several species associated with artificial clearings. Some of them, such as the cerambycids *Corymbia rubra*, *Prionus coriarius*, *Rhagium bifasciatum* or *Anastrangalia sanguinolenta* live in old stumps and are favoured by those left in the artificial clearings after cutting.

Species living in small branches seem also favoured by the branch heaps left in artificial clearings after cutting. The little cerambycid *Stenurella melanura* seems to favour particularly these structures. This species is abundant everywhere but particularly in artificial clearings. According to HORION (1974), *Stenurella melanura* lives in rotten branches on the ground. To a lesser extent, species living in little branches such

as *Pogonocherus hispidulus*, *Agrilus olivicolor*, *Anthaxia similis*, *Leiopus nebulosus* and *Obrium brunneum* also seem to be favoured by artificial clearings.

RELATIONSHIPS BETWEEN BEETLE COMMUNITIES AND FOREST MANAGEMENT

Taking a closer look at axis 2, we can notice that the opposition between "artificial clearing" and "natural edge" is linked to another opposition: mixed forests against pure forests. This can be explained by a management adapted to each stand type. Sites 1, 4, 8, 9 and 10 on the top of the diagram are located in pure oak or beech forests, while the other sites are in mixed forests with a certain amount of coniferous trees. This is shown on the bottom of the diagram, by a higher number of species, living mainly in coniferous trees such as the cerambycids *Corymbia rubra*, *Anastrangalia dubia*, *A. sanguinolenta*, *Gaurotes virginea*, *Rhagium bifasciatum* and *R. inquisitor*, as well as the buprestids *Anthaxia similis*, *A. quadripunctata* and *A. helvetica*.

In our study area, mixed forests are mainly situated on thin calcareous soils which are unfavourable to the growth of most trees. Pine is the only species which grows quite well under these conditions. It requires much light for its growth and artificial clearings are necessary to favour it. This explains why artificial clearings are opened mainly in this type of forests.

In our study area, pure beech forests are usually located above 800 m, on deeper and more fertile soils. As beech is a shade species, beech forest management does not require the opening of large artificial clearings. These forests are usually quite dark as beech canopy is very thick and their beetle fauna is generally poorer than in mixed or oak forests.

On the contrary, oak forests usually grow below 700 m and young trees need a lot of light for their growth. The management of this type of forests implies the opening of artificial clearings. Unlike beech, oak hosts a large number of specific insect species, much more related to the tree itself than to the forest structure. This explains the position of our site 4, an artificial clearing in a pure oak stand. Its fauna is closer to that of site 1, located at the edge of a pure oak forest, than to the other artificial clearings in mixed stands.

In normally managed forests, most of the trees are cut before reaching an age where the foliage becomes scarcer. A forest of healthy trees is therefore very dark, a feature not favourable for the studied fauna which is thermophilous. To a certain extent, we can consider artificial clearings as a substitute to natural clearings caused in primeval forests by the fall of old trees, all the more so that in addition to the light and the heat they cause, they also provide suitable biotopes for larvae as long as stumps and branch heaps are left on the site. These stumps and branches are more attractive in sunny places, than in dark places deeper in the woods, since not only the adults but also the larvae are thermophilous. This suggests that a careful management respecting local conditions can enhance forest beetle diversity.

Apparently, edge beetle assemblages are rather constituted of species living in herbaceous plants. They would be very sensitive to any edge and surrounding modification, be it a reduction of the edge width or a change in the agricultural practices.

For instance the replacement of a meadow by a field would change the microclimate, suppress an important food source and probably increase chemical treatments.

The results therefore suggest that the link existing between the type of forest and the kind of management is reflected by the beetle communities.

CONCLUSION

This study shows that the main factor for the presence of xylophagous beetles is the occurrence of their host plants. This concerns chiefly 9 species which are strongly dependant on their host plant. In our case, the species in question are mainly linked to oak and would be very sensitive to a vegetation change. Therefore, this tree of high biological value, hosting many typical species, has to be maintained. It should also be favoured by adapted management.

The second main factor found in our study is the ecotone structure. Species found in artificial clearings are not the same as those trapped in natural edges.

In order to preserve in our forests a diversified beetle fauna including specialized species, it is important to keep the number of indigenous trees adapted to site conditions as high as possible, among them oak. In a mountainous country like Switzerland, oak is not a very common tree since most of the lowlands are intensively cultivated. It is therefore important to favour this species where it is possible. At higher altitude, beech often constitutes monospecific stands. Tree diversity could be enhanced by favouring other species such as linden (*Tilia* sp.) or maple. Diversified structures must also be maintained. Even if artificial clearings have a favourable effect when stumps and branch heaps are left after the cutting, one must keep in mind that they cannot replace natural edges. These have to be maintained where they already exist and encouraged elsewhere in favourable sites. It has also to be recalled that artificial clearings favouring pine have a very favourable effect when young trees are small. Nevertheless, their area should remain limited because the rich mixed forest should not be replaced little by little by a pine monoculture.

ACKNOWLEDGEMENTS

I would like to express my deep gratitude to Prof. W. Matthey and Dr D. Borcard for guiding this study, to Dr J. Gutowski for reviewing this manuscript, to E. Mitchell for correcting the English text and to P. Junod and M. Plachta for collaboration.

REFERENCES

- ALLENSPACH, V. 1970. Coleoptera: Scarabaeidae, Lucanidae. *Insecta helvetica*, Catalogus 2, 186 pp.
- BARBALAT, S. 1995. Efficacité comparée de quelques méthodes de piégeage sur certains Coléoptères saprophages ou xylophages et influence de l'anthophilie sur le résultat des captures. *Bulletin de la Société neuchâteloise des Sciences Naturelles* 118: 39-52.

- BARBALAT, S. 1996. Influence de l'exploitation forestière sur trois familles de Coléoptères liés au bois dans les Gorges de l'Areuse (Canton de Neuchâtel, Suisse). *Revue suisse de Zoologie* 103 (2): 1-12.
- BARBALAT, S. 1997. Faunistique de 47 Cérambycides (Col. Cerambycidae) capturés dans les Gorges de l'Areuse (Neuchâtel, Suisse). *Bulletin de la Société neuchâteloise des Sciences Naturelles* 120: 99-119.
- BARBALAT, S. & BORCARD, D. 1997. Distribution of four beetle families (Coleoptera Buprestidae, Cerambycidae, phytophagous Scarabaeidae and Lucanidae) in different forest ecotones in the Areuse Gorges (Neuchâtel, Switzerland). *Ecologie* 28 (3): 199-208.
- BENSE, U. 1995. Longhorn beetles. An illustrated key to the Cerambycidae and Vesperidae of Europe. *Margraf, Weikersheim*, 512 pp.
- DAJOZ, R. 1980. Ecologie des insectes forestiers. *Bordas, Paris*, 489 pp.
- GEISER, R. 1984. Rote Liste der Käfer. In: BLAB, J., NOWAK, E., TRAUTMANN, W. & SUKOPP, H. (eds). Rote Liste der gefährdeten Tiere und Pflanzen in der Bundesrepublik Deutschland. *Naturschutz Aktuell* 1. Kilda. Greven, 270 pp.
- GUTOWSKI, J. 1985. Distribution of cerambycid beetles (Coleoptera: Cerambycidae) in various forest site types in Białowieża Primeval Forest. *Parki Narodowe i Rezerваты Przyrody* 6 (1): 77-94. (in Polish)
- GUTOWSKI, J. 1986. Species composition and structure of the communities of longhorn beetles (Col., Cerambycidae) in virgin and managed stands of Tilio-Carpinetum stachysetosum association in the Białowieża Forest (NE Poland). *Journal of Applied Entomology* 102: 380-391.
- GUTOWSKI, J. 1995. Changes in communities of longhorn and buprestid beetles (Coleoptera: Cerambycidae, Buprestidae) accompanying the secondary succession of the pine forests of Puszcza Białowieska. *Fragmenta Faunistica* 38 (20): 389-409.
- HARTMANN, K. & SPRECHER, E. 1990. Ein Beitrag zur Insektenfauna des Arlesheimer Waldes unter Berücksichtigung der Holzbewohnenden Käfer. *Tätigkeitsberichte der Naturforschenden Gesellschaft Baselland* 36: 75-124.
- HORION, A. 1958. Faunistik der mitteleuropäischen Käfer. Band 6: Lamellicornia. *Selbstverlag, Überlingen*, 343 pp.
- HORION, A. 1974. Faunistik der mitteleuropäischen Käfer. Band 12: Cerambycidae - Bockkäfer. *Selbstverlag, Überlingen*, 228 pp.
- KOCH, K. 1992. Die Käfer Mitteleuropas, Ökologie. Band 3, *Goecke & Evers, Krefeld*, 389 pp.
- LOHSE, G. A. & LUCHT, W. 1992. Die Käfer Mitteleuropas. Band 13, *Goecke & Evers, Krefeld*, 375 pp.
- SPEIGHT, M. 1989. Les invertébrés saproxyliques et leur protection. *Collection sauvegarde de la nature* 42, Strasbourg, 77 pp.
- STARZYK, J. 1976. Grouping of cerambycids (Coleoptera, Cerambycidae) on the background of types of environment of the Niepolomice Forest near Krakow. *Acta Agraria et Silvestria, Series Silvestris* 16: 131-152. (in Polish)
- STARZYK, J. 1977. Influence of the stand age upon the quality of the composition and the numerousness of the timber beetles (Col., Cerambycidae) in the Niepolomice Forest. *Acta Agraria et Silvestria, Series Silvestris* 17: 117-135. (in Polish)
- STARZYK, J. 1979. Cerambycidae communities (Col. Cerambycidae) occurring in various phytosociological forest types of Niepolomice Forest near Krakow. *Journal of Applied Entomology* 88: 44-55.
- STARZYK, J. & WITKOWSKI, Z. 1981. Changes of the parameters describing the cambio- and xylophagous insect communities during the secondary succession of the oak-hornbeam association in the Niepolomice Forest near Krakow. *Journal of Applied Entomology* 91: 525-533.

- TER BRAAK, C. J. F. 1986. Canonical correspondence analysis. A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- TER BRAAK, C. J. F. 1988a. Partial canonical correspondence analysis (pp. 551-558). In: Block, H. H. (ed.). Classification and related methods of data analysis. *North Holland Press, Amsterdam*.
- TER BRAAK, C. J. F. 1988b. CANOCO - an extension of DECORANA to analyze species-environment relationships. *Vegetatio* 75: 159-160.